1° 21′ S. lat, except for the depth of the body, which is $4\frac{1}{2}$ to $4\frac{2}{3}$ times in the total length, the maxillary not extending quite to below the anterior border of the eye, the diameter of which is $4\frac{1}{2}$ times in the length of the head. 9 gill-rakers on lower part of anterior arch. D. XV-XVI 9; A. III 8–9; Sq. 30–32 $\frac{4-5}{12-13}$; Lat. l. 20–21/13–14. 6 or 7 scales between the first dorsal spine and the lateral line.

Smaller specimens (85–95 millim.) differ in the smaller head, the larger eye ($3\frac{1}{2}$–4 times in length of head), and the lower jaw not projecting beyond the upper. The dark longitudinal bands are very indistinct and are traversed by 7 or 8 ill-defined dark cross-bars.

In all the specimens the ventral fins are of a bright yellow.

3. On the Structure and Affinities of *Udenodon*.

By R. Broom, M.D., B.Sc.[1]

[Received May 21, 1901.]

(Plates XVI.–XVIII.)[2]

(Text-figures 10 & 11.)

A considerable number of skulls of *Udenodon* and of the closely allied genus *Dicynodon* have long been known, and there have also been found many other bones of the skeletons; but as in almost all the specimens the association of the skull and other bones has been quite lost, it is at present impossible to refer limb-bones to their proper species of which the skulls are the types, and it is only with some doubt that they can be referred even to their proper genera. In a few cases some bones of the skeleton have been found in association with *Dicynodon*-skulls, but in the case of *Udenodon* the post-cranial skeleton is quite unknown.

The most important specimen in which the Dicynodont skull is in association with a considerable portion of this is the little form which has been described by Seeley (1) as "*Keirognathus cordylus*." In this specimen the skull, upper vertebræ and ribs, front limbs, shoulder-girdle, and sternum are shown, but all in a very bad state of preservation. There is scarcely a doubt that the skeleton is that of a young *Dicynodon*, and it is specially valuable as showing the relations of the shoulder-girdle, sternum, and interclavicle. Seeley's restoration is unsatisfactory.

In the Lower Karroo beds of Pearston, S. Africa, while the remains of various species of *Dicynodon* are met with, the genus which most commonly occurs is *Udenodon* and from the specimens which I have recently discovered I am now in a position to give an almost complete account of its skeleton.

[1] Communicated by Prof. G. B. Howes, LL.D., F.R.S., F.Z.S.

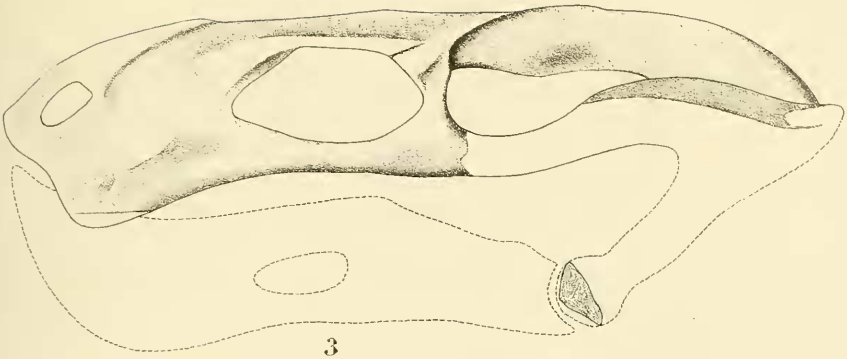
[2] For an explanation of the Plates, see p. 190.

1

R.B del.
M.P.Parker lith.

Parker & West imp.

SKELETON OF UDENODON GRACILIS.



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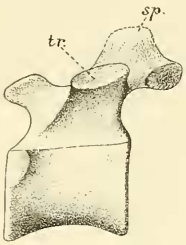

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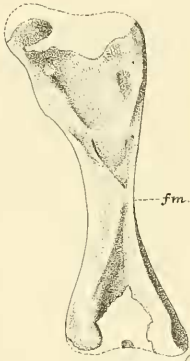

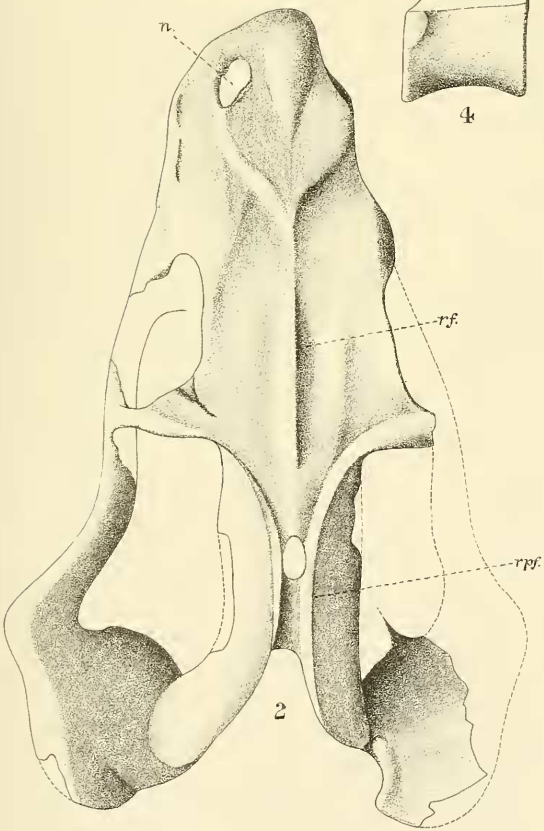

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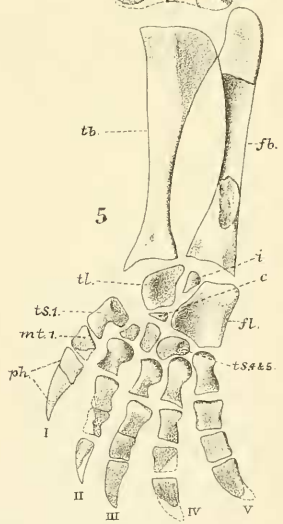
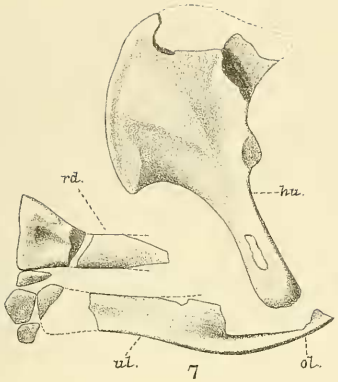


5

R.B del.
M.P.Parker lith.

Parker & West imp.

SKULL, VERTEBRA, & HIND LIMB OF UDENODON.



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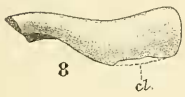

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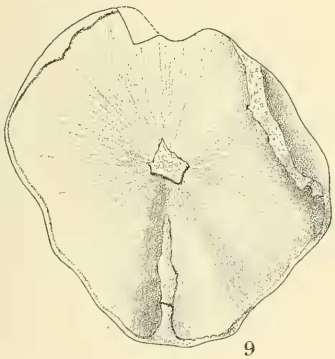

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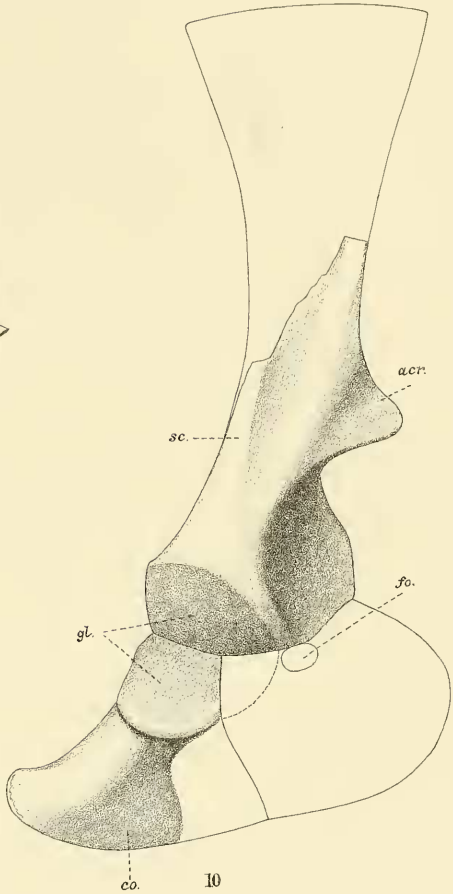

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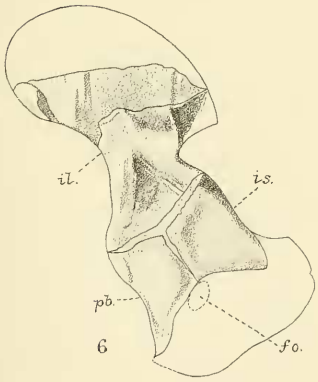

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11

R.B del.
M.P Parker lith.

Parker & West imp.

LIMB-BONES & STERNUM OF UDENODON.

When an endeavour is made to classify the specimens found, one is beset with a number of difficulties. Almost every specimen exhibits some degree of crushing; and when two skulls of the same species have been crushed in different directions, the appearances would readily make one believe that he was dealing with two species. One skull of *Udenodon baini* in my possession has the maxilla of one side so crushed as to give an appearance very like that in the specimen described by Owen (2) as "*Udenodon strigiceps*." Another difficulty is due to our ignorance of the extent to which differences in specimens may be due to the sex and age. The identification of any specimen therefore must in the meantime be subject to some doubt.

The following is a list of the specimens which I have found and on which my researches are based:—

1. An almost complete skull of a small form, which I regard as new, and for which I propose the name of *Udenodon gracilis* (Pl. XVII. figs. 2 & 3).
2. An almost perfect skeleton of apparently the same species. The skull unfortunately has been so much weathered that it is impossible to decide the species with certainty (Pl. XVI.).
3. A lower jaw of possibly the same species.
4. A fairly good skeleton of *Udenodon baini*.
5. A second very imperfect skeleton of presumably the same species, but with the head missing.
6. A moderately complete skull of *Udenodon baini*, but much crushed on one side.
7. A second imperfect and much crushed skull of the same species.
8. A third imperfect skull, also probably of *U. baini*.
9. A moderately complete but somewhat crushed skull of a young animal, probably *U. megalops*. From a much higher stratum than the other specimens.
10. An imperfect skull of a young animal, apparantly *U. greyi*.
11. The posterior portion of a skull referred to *Udenodon*, but possibly belonging to a *Dicynodon*.
12. The mandible and front part of snout of a small *Udenodon*.
13. Imperfect middle region of a small *Udenodon*-skull.
14. A number of detached portions of mandibles, maxillæ, humeri, vertebræ, and other bones referred to *Udenodon*.

Of these specimens all have been discovered in the neighbourhood of Pearston, S. Africa, with the exception of specimen 10, which is from the Bedford district and was kindly presented to me by Mr. D. D. Frazer, Junr.

Before beginning an account of the general structure of *Udenodon*, I think it will be well to give a brief description of specimens 1 and 2.

The small skull which I take as the type of *Udenodon gracilis* (Pl. XVII. fig. 2) is somewhat crushed on the right side, and

on the same side the temporal arch and the lower jaw are missing, but otherwise the skull is almost perfect. The skull is more elongated than is usual in *Udenodon*, and differs from most species in having the interorbital region very considerably wider than the parietal region. The eyes are moderately small and directed more outwards than upwards. The nostrils (*n.*) are placed far forwards and rather small. The nasal bones are prominent immediately behind the nostrils. The caniniform ridges are flat and slender and directed well forwards. The suborbital arch is moderately round and rather feeble. The frontal region is broad and moderately flat, and is characterized by a rather prominent median ridge (*r.f.*). Posteriorly, the frontals are considerably wider than in front. The postfrontals, where they join the frontals are flat and broad and to a considerable extent roof over the orbits. Externally they are rather slender. A distinct ridge runs from the posterior border of the postorbital portion of the postfrontal bone inwards, then backwards along the posterior part of the postfrontal. The parietal region is about two-thirds the width of the frontal region, and is characterized by the presence of two well-marked postfrontal ridges (*r.p.f.*), with an intervening depressed parietal portion. The squamosals are large, and the anterior portions which form the temporal arches are developed considerably, horizontally outwards.

The second specimen (Pl. XVI. fig. 1) referred to is an almost perfect skeleton of a small *Udenodon*, and it is especially valuable in that the bones are scarcely at all displaced. The specimen was found in an impure and fairly hard shale. The skull had evidently been long exposed, and is so badly weathered that very little now remains of the bones of the upper side of the head. The post-orbital arches are quite lost, though evidences of their positions are given by the underlying matrix. The squamosal, so far as it is displayed, agrees very closely with that in *Udenodon gracilis*, and nothing in the other parts of the head seems to oppose this determination.

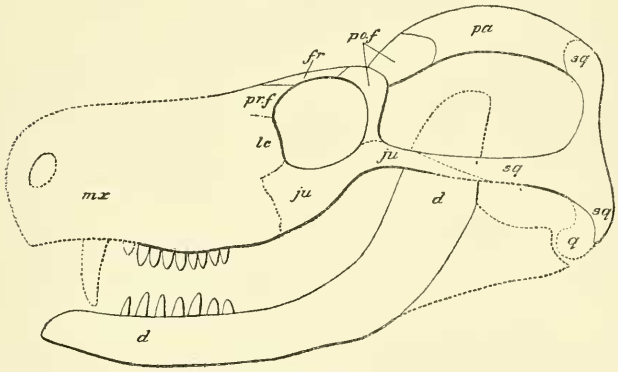
When the slab in which the skeleton lay was split, it was found that this had been so arranged that the remains were almost equally divided between the two sides. In the larger of the two portions, which may be looked upon as the main slab, are preserved the almost perfect left fore-limb, the impressions of a number of vertebræ, a large number of ribs and impressions of ribs, the sacrum and caudal region, the left ilium (*il.*), and the left hind-limb, which unfortunately is twisted and has not been fully displayed, and the right ischium (*is.*) and pubis (*pb.*). In the counterpart slab is seen the head, the right fore-limb, almost all the vertebræ and ribs, and the right ilium with the right hind-limb extended and almost perfectly displayed. In the drawing (Plate XVI.) the bones and impressions on the main slab are with the skull figured and shaded in true relative position, while the bones of the counterslab are in outline in proper relationship with those of the main slab.

In the following account of the structure of *Udenodon*, that part dealing with the skull is founded mainly on the skulls I have obtained at Pearston, while the account of the post-cranial skeleton is mainly based on the little skeleton of *Udenodon gracilis*.

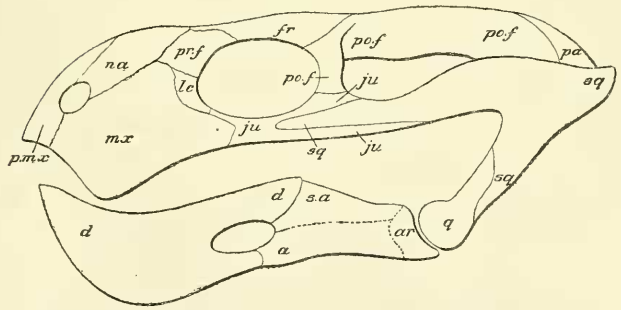
Skull.

The Dicynodont skull has been described by Owen (2), Cope (3), Huxley (4), and others, but the fullest description is that given by Seeley (5). Even Seeley's account, however, leaves many points in doubt, and a considerable number of his determinations are very questionable. I have therefore thought it well to give an independent description of the skull, dealing but briefly with those elements whose structure is well known, and more fully with the points open to dispute.

Text-fig. 10.



Text-fig. 11.



A composite figure of the skull of *Udenodon* (text-fig. 10) showing details from the left side, for comparison with the skull of a primitive Theriodont, *Ictidosuchus primævus* (text-fig. 11).

a., angulare; *ar.*, articulare; *d.*, dentary; *fr.*, frontal; *ju.*, jugal; *lc.*, lachrymal; *mx.*, maxilla; *na.*, nasal; *pa.*, parietal; *p.mx.*, premaxilla; *po.f.*, post-frontal; *pr.f.*, prefrontal; *q.*, quadrate; *sq.*, squamosal; *s.a.*, surangulare.

In *Udenodon* (text-fig. 10, p. 167) the whole beak has had a horny covering, which in some species at least covers not only the alveolar margin, but almost the whole of the facial surface of the maxilla (*mx.*); and in probably in all the species the horny layer was specially developed over the caniniform development of the maxilla.

The premaxilla in *Udenodon* and *Dicynodon* is better developed than in the majority of reptiles, having not only a well-developed facial portion passing up between the two nostrils, but also a large palatal portion. The two premaxillæ, as in the bird, must have very early united into a single bone (*cf.* Pl. XVII. fig. 2), as in even comparatively young specimens there is no trace of a suture between the two elements. As I have elsewhere shown (6), the premaxilla forms almost the whole of the bony palate, including by far the greater part of the median ridge, which has almost invariably been regarded as the vomer. In the paper referred to, a section through the posterior part of the hard palate of *Udenodon truncatus* is figured, and it is there shown that though the maxillæ have internal plates which form a sort of secondary palate, these are almost completely covered by the great palatal development of the premaxilla. From the palatal portion of the premaxilla there passes up internally a prominent median ridge which runs from the facial portion of the premaxilla backwards to articulate with the vomer, and to a considerable extent divides the nasal cavities.

The maxilla differs in shape greatly in different genera, and it is highly probable that there is considerable difference in shape in the two sexes of the same genus. In all, however, there is a more or less well-marked caniniform development. In some species a prominent external descending ridge gives the tusk-like development a triangular shape; in others the descending process is almost flat. The maxilla resembles that of man in having a large *antrum maxillare*. From the region of the antrum, which may be regarded as the centre of the bone, the maxilla is developed upwards, forming the greater part of the side of the snout (*cf.* text-fig. 10, p. 165) and bounded by the nostril and the nasal (*na.*), the prefrontal (*pr.f.*) and the lachrymal (*lc.*) inwards, forming part of the secondary palate; and backwards, meeting the jugal, are the palatine and the pterygoid bones. The caniniform ridge is continued back into the ridge formed by the anterior bar of the pterygoid and forms the border of the palate.

I can find no evidence of any ossified turbinal bones.

The nasals (*na.*) are moderate-sized bones irregularly triangular in shape. They are joined to each other by a fairly long median suture. Their anterior sides are formed by the premaxilla (*p.mx.*), the nostrils, and the maxillæ. The posterior and outer side of each nasal is bounded by the frontal (*fr.*), the prefrontal (*pr.f.*), and maxillary (*mx.*).

The lachrymal (*lc.*) is quite mammalian in structure. It forms a considerable part of the anterior wall of the orbit—fitting in

between the prefrontal above and the jugal (*ju.*) below. It has a large lachrymal canal opening within the orbit.

The prefrontal (*pr.f.*) is a somewhat quadrate bone—three sides being formed by the orbit, the frontal, and nasal respectively, and the fourth side by the lachrymal and maxilla. It forms a considerable portion of the anterior and upper wall of the orbit.

The frontals (*fr.*) lie between the orbits and are usually well developed. In *Udenodon greyi* they are narrow; in *U. gracilis* almost exactly as broad as long. They usually form the borders of the upper sides of the orbits. Each frontal articulates with the nasal and prefrontal in front, and with the parietal and postfrontal behind.

The postfrontal (*po.f.*) forms, as in *Dicynodon* and many Theriodonts, an outer limb which forms the postorbital arch, and a posterior which runs backwards by the side of the parietal. The postorbital arch varies considerably in different species, but is usually rather broad above, forming a sort of roof to part of the orbit. In the middle it is generally narrow and round; while inferiorly it broadens out and articulates with the squamosal and the jugal. From the upper end of the postorbital portion the posterior part runs abruptly backwards, forming the greater part of the inner wall of the temporal fossa, and to a great extent hiding the parietal. Posteriorly it curves outwards a little and meets the squamosal (*cf.* text-fig. 10, p. 165).

The parietals early unite to form a single bone, which though of moderate size is very largely hidden by the postfrontals. Near the centre of the bone is a fairly large parietal foramen. Posteriorly the parietal articulates in the middle with the interparietal, and laterally with the squamosals (*sq.*).

The jugal is rather a small bone (*ju.*) which forms the greater part of the infraorbital arch. Anteriorly it forms a considerable part of the wall of the orbit at its anterior and lower side, meeting the lachrymal and being clasped by the maxilla. Internally, the anterior part meets the palatine. The squamosal (*sq.*), which lies on the outer side of the jugal in its middle and posterior regions, to a large extent hides it from view. Where the jugal meets the postfrontal it is fairly deep in some species, but in others only slightly increased in depth. Posteriorly it flattens out and lies on the inner side of the squamosal, forming with it the temporal arch.

The squamosal is by far the largest bone in the skull (*cf. sq.*, text-fig. 10, p. 165). It comprises a large broad posterior portion which descends from its union with the parietal and postfrontal, along the outer border of the supra- and exoccipitals, to give articulation to the quadrate, and an anterior branch, which springs from the upper half of the posterior portion and passes forwards to form with the jugal the temporal arch.

The quadrate (*q.*) consists of a broad flat part which lies against the front of the descending portion of the squamosal, and a large articular head. The articular face of the quadrate has a deep

antero-posterior groove running across it, which divides it into an outer semicircular button-like portion and an inner very prominent antero-posterior ridge. Both the outer and inner portions of the articular face have an antero-posterior convexity of fairly wide radius.

The structure of the palate I have elsewhere dealt with (6), and I have little further so add to my previous description. The pterygoids, as in the other Dicynodonts, are greatly developed, meeting each other in the middle line and sending processes forwards to the maxillæ and backwards to the quadrates. Between the two anterior processes lie the palatines and the vomer. The vomer is quite mammalian in structure, and is present as a median plate, extending from the fork formed by the anterior branches of the pterygoids forwards to articulate with the palatal median and internal median ridges of the premaxilla. Superiorly the vomer articulates with the sphenoid, the mesethmoid, and the ethmoid cartilage. Towards the posterior and upper part it gives off a pair of small lateral wings which articulate with the palatines, and with them form the roofs of the nasal passages. The palatines pass outwards and downwards from the articulations with the vomer, by the side of the anterior branches of the pterygoids. Each palatine then sends a process forwards and inwards to form a sort of rudimentary secondary palate, and a second process outwards above the anterior lobe of the pterygoid to meet the jugal.

Where the two pterygoids meet in the middle line they rest on, and are articulated to, the basisphenoid. This latter bone shows on the under surface of the skull to a considerable extent, sending two plates backwards to clasp the large paroccipital processes. From the region where the pterygoids meet, the basisphenoid sends a comparatively narrow median plate upwards and forwards resting on the vomer, and probably in adult specimens articulating with the mesethmoid. This plate may be the presphenoid, but I have not seen any specimens in which it is distinct from the basisphenoid. The mesethmoid is a median plate which forms the greater part of the interorbital septum. Above it is clasped by the orbital plates of the frontals, and below it rests on the vomer.

Immediately behind the point where the pterygoids meet, there passes upwards from each pterygoid a slender *columella cranii*. In forms with a deep narrow skull, e.g. *U. greyi*, the columella is long and slender: in those species where the skull is broad and rather flat, the columella is comparatively short. In all forms, however, it is very slender. It appears to articulate with the parietal above.

The periotic bones appear to form the lateral walls of the braincase in a manner very similar to that seen in lizards; but I have not seen any specimens in which their exact limits could with certainty be determined.

The occiput has long been well known in a number of Dicynodonts, especially *Ptychosiagum*. A small occiput is figured by

Lydekker in the British Museum Catalogue of Fossil Reptiles, which is probably that of a species of *Udenodon*. The supra- and exoccipitals are bordered by the interparietal and the squamosals, while the lower corners of the large exoccipital processes also articulate with the quadrates.

Between the quadrate and the descending process formed by the exoccipital and basioccipital, there lies a remarkable little dumbbell-shaped bone, which with one end fits into a hollow of the occipital process and with the other supports the quadrate. As it is but loosely articulated, it is lost from the majority of *Dicynodon* and *Udenodon* skulls discovered. This bone differs so markedly from any bone found in the posterior region of the skull in known Reptiles or Mammals, that one hesitates in giving an interpretation. As, however, it forms with the notch in the lower border of the exoccipital an oval aperture, and as the columella auris lies in this same notch of the exoccipital, it seems to me most probable that it is the homologue of the mammalian tympanic.

Lower Jaw.

The lower jaw is almost typically reptilian in structure (*cf.* text-fig. 10, p. 165). In front, the two large toothless dentaries (*d.*) are anchylosed together as in the tortoise. Each dentary is considerably deeper than in the tortoise, and differs in forming a single edge above, instead of two ridges as in the Chelonian. In *U. greyi* the outer surface of the dentary is moderately flat; but in *U. gracilis* there passes outwards from the posterior part of the bone a very prominent horizontal ridge. On passing backwards the dentary divides into an upper and a lower lobe, which meeting respectively the surangular (*sa.*) and the angular (*a.*) encloses with these a fair-sized oval vacuity. The angular is a rather large flat element which articulates with the dentary in front, the surangular above, the splenial below, and the articular (*ar.*) behind. The surangular is a fairly strong bone which fits into a deep cavity in the posterior end of the upper part of the dentary. The splenial extends along almost the whole length of the jaw, from the articular behind to the symphysis in front. Posteriorly it is fairly stout, but on passing forwards it becomes a rather thin plate. The articular is a large thick bone, but, as in Chelonians, short.

I am unable to give any account of the hyoid apparatus, as though there are evidences of hyoid bones, they are disconnected and their interpretation is quite uncertain.

Vertebræ.

In the little skeleton of *Udenodon gracilis* (Pl. XVI.) most of the vertebræ are preserved, but none are well displayed. The atlas and axis are hidden by matrix, but from the 3rd cervical (4th?) there are indications of almost all the other vertebræ. The skeleton does not show where the division lies between the cervical and

the thoracic series; and in *Udenodon*, as in most other Theromorphous reptiles, there is no division of the body vertebræ into thoracics and lumbars. Assuming that the first cervical vertebra displayed is the 3rd cervical, then it is moderately certain that in *U. gracilis* there are 27 presacral vertebræ.

The vertebræ which I take to be 3rd and 4th cervicals, so far as displayed, agree fairly closely with the 3rd and 4th cervicals of *Tropidostoma dunni* Seeley (5) [=according to Lydekker (7) *Ptychosiagum microtrema* Seeley]. The bodies of the vertebræ have well-marked lateral processes arising from the anterior and outer angles of the ventral surfaces, for articulation with the cervical ribs.

In the skeleton of *Udenodon gracilis*, though most of the vertebræ of the thoraco-lumbar series are shown, unfortunately only the bodies are displayed; but in the imperfect skeleton of *U. baini* (spec. 4) a number of presacral vertebræ are well preserved.

As has long been known in other Dicynodonts, the vertebræ consist of deeply cupped bodies to which are articulated arches closely resembling the arches in mammals. In the dorsal series (*cf.* Plate XVII. fig. 4) the bodies are considerably elongated and moderately constricted in the middle. On the body just below the neuro-central suture in front is the articular surface for the head of the rib. The pedicle is stout, and a ridge runs up obliquely from near the front of the neuro-central suture to the transverse process. The transverse processes (*tr.*) are short and strong, directed outwards and slightly upwards, and lie well above the level of the top of the neural canal. The spine (*sp.*) is quite short, and situated well backwards over the posterior zygapophyses. Both the anterior and posterior zygapophyses are situated fairly closely together, and the articular surfaces make approximately a right angle with each other. A large opening is formed between each pair of vertebræ for the exit of the spinal nerves.

The ribs in the thoracic region (*cf.* Plate XVI.) are long and slender; the anterior ones being, however, slightly stouter than the others. The upper end of the rib is expanded so as to form a distinct head for articulation with the centrum and a tubercle for attachment to the transverse process. As the border of the rib between the head and the tubercle is almost straight, and the ridge on the vertebra between the articular surface and the transverse process is only slightly concave, there must be but little of a foramen left between the rib and the vertebra. The ribs in the lumbar region have their upper ends less expanded and may possibly have been articulated to the transverse processes alone.

The sacrum is very badly preserved in the skeleton of *U. gracilis*, but appears to have been composed of 5 vertebræ.

The tail has evidently been short, but it is impossible to say of how many vertebræ it may have been composed. Those that

are shown in the little skeleton have their centra about half the length of those in the thoracic series. The vertebræ are much crushed and fractured, so that it is difficult to be certain of the identification of the fragments. By the side of one of the vertebræ is a well-developed process, which may be a spine, but which I am rather inclined to believe to be an autogenous transverse process.

Shoulder-girdle and Sternum.

In the little skeleton of *Udenodon gracilis* the shoulder-girdle, though present, is almost completely hidden by matrix and could not be displayed without injury to other parts. In the skeleton of *U. baini* (spec. 4, Pl. XVIII. fig. 10) the scapula (*sc.*), precoracoid (*p.co.* fig. 11) and coracoid (*co.*) are well preserved, and also in the very imperfect skeleton (spec. 5), while in specimen 5 the sternum is also shown.

The scapula, precoracoid and coracoid agree pretty closely with the corresponding bones in the Dicynodont shoulder-girdle as figured by Owen (2), Seeley (1), and Lydekker (7). The scapula is somewhat stouter than that figured by Lydekker, but on the whole closely agrees with it. The upper part of the scapula is broad and flat and only moderately curved inwards. The anterior border is grooved for the lodgment of the cleithrum. A little below the middle of the scapula there is a well-marked acromion process (*ac.*, Pl. XVIII. fig. 10) which passes forwards, upwards, and slightly inwards as a fan-like expansion. The lower end of the scapula has a large glenoid surface (*gl.*) which looks downwards and a little outwards, and an anterior flattened continuation which articulates with the precoracoid.

The coracoid (*co.*) is comparatively small, but has a large glenoid surface (*gl.*) which looks mainly outwards, and which is separated from the outer surface of the bone by a very prominent bony border.

The precoracoid (*p.co.*) is a moderately flat bone, but slightly larger than the coracoid. On its upper border is a deep notch (*fo.*) which closed by the lower border of the scapula becomes a large oval foramen. The precoracoid articulates behind by a straight suture with the coracoid, and above with the scapula. It appears to furnish a small portion of the glenoid cavity.

I have failed to identify the interclavicle or cleithrum in any of the specimens in my possession, but in the skeleton of *U. gracilis* one of the clavicles is fairly complete (*cl.*, Pl. XVI. & Pl. XVIII. fig. 8). It is curved very much like the human clavicle. It appears to have articulated with its neighbour in the middle line, and to have rested on the anterior part of the interclavicle. The inner half of the bone is flattened antero-posteriorly, and the outer vertically.

The sternum, or perhaps more correctly præsternum (Pl. XVIII. fig. 9), is a moderately large four-sided median plate, with the angles pointing forwards, backwards, and to the sides. The

anterior angle is notched, probably for the lodgment of the interclavicle; the outer angles are rounded and the posterior angle truncated as if to give attachment to a cartilaginous meso- or xiphisternum. For its lower two-thirds there is a well-marked median ridge for the attachment of the pectoral muscles. The bone is a little longer than broad.

Humerus.

In the little skeleton of *Udenodon gracilis* (Pl. XVI.) one of the humeri (*hu.*) is perfectly preserved and beautifully displayed; the other though less perfect has the opposite side showing. In specimen 4 one humerus is fairly well preserved, and of the other the lower half is almost perfect; while in specimen 5 one humerus is shown, but in bad condition. The difference between the humeri in *U. gracilis* and *U. baini* is very striking, and much greater than one could have expected to find in two species apparently so closely allied.

In *Udenodon gracilis* (Pl. XVI.), the humerus, while constructed on the well-known Dicynodont type, is characterized by a number of peculiarities. The delto-pectoral crest (*c.d.*) is greatly developed, its border curving forwards and downwards from the articular surface and ending, as in "*Platypodosaurus robustus*," in a somewhat hooked process. The ento-tuberosity is developed to a greater extent than is met with in the humerus of any S. African reptile hitherto discovered, and forms a long flattened tapering process which ends in a rather sharp point. Near the middle of the bone on its inner side is developed a very prominent tricipital ridge resembling more that seen in *Echidna* than the rounded prominence on the humerus of "*Platypodosaurus*." The articular surface of the head of the bone resembles greatly that in *Ornithorhynchus* and *Echidna* in being considerably developed transversely, while it is but very narrow. As in the Monotremes, a sharp ridge runs down from the articular head to the external condyle; and this is very peculiarly developed, in that while in the humeri hitherto discovered though it may be very prominent it is generally slender, it is here a markedly rounded boss (*c.e.*). The internal condyle is not very large. The entepicondylar foramen is only of moderate size, and is situated a little more distally than is usually the case in Dicynodonts. The ridge of bone which forms the bridge over the foramen runs up to the base of the delto-pectoral crest.

In *Udenodon baini* the humerus varies much less from the normal dicynodont type. The delto-pectoral crest is not developed downwards to form a hooked process in front; the tricipital ridge appears to have been small; while the external condyle is not more greatly developed than is the case in *Ornithorhynchus*.

Radius and Ulna.

The radius and ulna are very mammal-like in form (*cf.* Plate XVI.).

The radius (*rd.*) is considerably shorter than the humerus. Its

upper half is moderately rounded, and from the head to a little below the middle of the bone it steadily decreases in thickness, so that at the middle the diameter is only about one-half that of the head. In its lower third the bone becomes flattened out to give a broad articulation to the radiale (*ra.*). The broad end of the bone has a deep depression on both its upper and under sides. Its articular surface looks downwards and slightly outwards.

The ulna (*ul.*) is very nearly twice as long as the radius, and considerably longer than the humerus; its great length being due to the greatly developed olecranon process (*ol.*; *cf.* also Plate XVIII. fig. 7). The upper half of the bone is very strongly developed, and the olecranon extends about as far beyond the sigmoid articulation as it does in such typical lowly mammals as the Wombat and the Porcupine. The point of the olecranon is directed slightly outwards, but it is not dilated like that of the Monotremes. On the outer side of the ulna a short prominent ridge is seen bordering the sigmoid articulation. On the inner side the upper part of the ulna is deeply excavated after the manner seen in that of *Echidna*, but to a much greater extent, as the border of the bone forms a much more prominent ridge. The lower half of the ulna is much flattened. Like the radius, the lower end is slightly expanded; while the articular surface looks slightly towards the radius.

Carpus (Plate XVI.).

In the skeleton of *Udenodon gracilis* the carpus is almost perfectly preserved, and the various bones composing it have scarcely been at all disturbed in position. In the proximal row are four bones—radiale (*ra.*) intermedium (*i.*), ulnare (*un.*), and pisiform (*pi.*); in the distal row are five carpals; while in the middle is a single centrale (*c.*).

The radiale or scaphoid (*ra.*) is a broad and considerably flattened bone which occupies the greater part of the articular end of the radius. Its dorsal surface shows a considerable depression towards its outer end. It articulates with the radius, with the 1st carpale, the centrale and the intermedium.

The intermedium or lunar (*i.*) lies between the end of the radius and the ulna and ulnare. On the upper side it has a fairly large surface, but on the under it is apparent as a slender plate fitting in between the radius and the ulnare.

The ulnare or cuneiform (*un.*) is considerably shorter in its transverse diameter than the radiale, but of much greater length antero-posteriorly. It articulates with the ulna, the intermedium, the 4th and 5th carpalia, the pisiform, and probably with the centrale. Bordering the side by which it articulates with the ulna there is a prominent little oblique ridge, and at the distal and inner corner of the bone is a little rounded eminence.

The pisiform (*pi.*) is a little bone which articulates with the outer side of the ulnare, and curves outwards and upwards, forming part of the articulation for the ulna.

The centrale (*c.*) is a rounded, moderate-sized element, which occupies the centre of the carpus. It articulates with the radiale, intermedium, and probably with ulnare of the proximal carpal bones, and with the 1st, 3rd, and 4th carpalia of the distal series. It is possible that a small second central element may have lain between the centrale and the ulnare, but I regard this as improbable.

The 1st carpale is a short flattened bone which fits in between the radiale and the 2nd carpale. On its outer end it gives an articulation to the pollex. Its inner end articulates with the 3rd carpale and the centrale.

The 2nd carpale is a very small bone which articulates with the 1st and 3rd carpalia, and supports the metacarpal of the 2nd digit, and possibly shares with the 1st carpale the support of the 1st metacarpal.

The 3rd carpale is a fair-sized element which fits in between the 2nd and 1st carpalia, the centrale, and the 4th carpale, and gives articulation to the 3rd metacarpal.

The 4th carpale is a large quadrangular element. Distally it gives articulation to the 4th metacarpal and to a slight extent to the 3rd and 5th metacarpals. Proximally it articulates with the centrale and the ulnare, and fits in between the 3rd and 5th carpalia.

The 5th carpale is very small, and is so closely articulated to the 4th carpale as to render it not improbable that the two elements may be anchylosed as age advances. In the little skeleton, which is probably immature but not very young, the two elements are quite distinct. The little 5th carpale articulates also with the ulnare, and gives articulation to the 5th metacarpal.

Metacarpals and Phalanges.

In the manus there are five well-formed digits, but I fail to detect any trace of a præpollex. The three median digits are somewhat stronger than the other two.

Of the pollex only the metacarpal and part of first phalanx are preserved. The metacarpal is a small rectangular bone about as broad as long. The 1st phalanx is probably very similar.

In the second digit, as in the first, only the metacarpal and a portion of the 1st phalanx are preserved. The metacarpal is a fair-sized element appreciably longer than broad. In the middle it is somewhat constricted, and at its distal end considerably expanded. The 1st phalanx was probably considerably smaller than the metacarpal.

The third digit is complete except the ungual phalanx. The metacarpal is very similar to that of the 2nd digit, but somewhat larger. Like the latter, it is constricted in the middle and expanded distally. The 1st phalanx is a quadrangular bone only slightly longer than broad, and slightly constricted in the middle. It is about one-half smaller than the metacarpal. The 2nd phalanx is very similar in shape to the 1st, but still smaller.

The fourth digit is almost perfect. The metacarpal is about equal in size to that of the 3rd digit, but is less constricted in the

middle. The 1st phalanx is a quadrangular bone slightly broader than long and only slightly constricted in the middle. The 2nd phalanx is a small bone very distinctly broader than it is long. It gives articulation to a large claw. The terminal or ungual phalanx is narrow, slightly curved, and almost as long as the metacarpal and the other two phalanges together.

The fifth digit has a small metacarpal, about as broad as long, and but slightly narrowed in the middle. The 1st and 2nd phalanges are both small quadrangular bones, the 1st being considerably smaller than the metacarpal, and the 2nd than the 1st. The ungual phalanx is almost as large as that of the fourth digit, and like it but slightly curved.

In *Udenodon baini* the metacarpals and phalanges appear to be very like those in *U. gracilis*, but the ungual phalanges are much shorter and broader, and the whole digits appear proportionally stronger.

Pelvis.

In the skeleton of *Udenodon gracilis* (Plate XVI. and Plate XVII. fig. 6) the almost perfect ilium (*il.*) is displayed. On the right side the ischium (*is.*) and pubis (*pb.*), with a portion of the ilium, are shown attached to the main slab, while the greater portion of the right ilium remains adherent to the counter slab.

The ilium resembles considerably the ilium of *Ptychosiagum orientale* figured by Lydekker (7) in being directed upwards and forwards, and in being greatly expanded antero-posteriorly. As the acetabulum (*ac.*) is fairly large, the lower end of the ilium which articulates with the pubis and ischium is broad. On passing upwards it becomes somewhat constricted into a short neck, from which it again rapidly broadens into a large fan-like expansion. The anterior part of the blade of the ilium lies much in advance of the axis formed by the neck and the acetabulum, the anterior border of the bone forming a graceful gentle curve forwards. The posterior part of the blade is of much less size, and the posterior border curves almost abruptly backwards from the neck and at right angles to its axis. The iliac blades are moderately flat, being only slightly concave antero-posteriorly on their outer side and with some muscular ridges.

The pubis (*pb.*) is peculiarly twisted, so that while the upper part looks outward the lower looks mainly downward. The pubis forms a little more than a quarter of the acetabulum, and bounds the articular cavity by a prominent ridge. The outward facing portion of the pubis is triangular in shape. In front of the acetabulum is a little prominence—apparently the pectineal tubercle; while at the lower and anterior angle of the triangular portion is another small tubercle, which in position corresponds with the tubercle which in *Ornithorhynchus* assists in the articulation of the marsupial bone. A ridge runs obliquely from this lower tubercle towards the lower border of the acetabulum, and from it the pubis passes at first directly inwards and then downwards and inwards. The exact size of the obturator foramen (*f.ob.*) is not clearly shown

in this skeleton, but it is situated immediately below the oblique ridge not far from the lower border of the acetabulum. The lower part of the pubis is moderately flat, and does not extend farther forward than the level of the lower tubercle. The anterior border between the lower tubercle and the symphysis is straight, as if for the articulation of a cartilaginous epipubic element. There is a long articulation between the pubis and the ischium below the obturator foramen.

The ischium (*is.*) in *Udenodon gracilis* is proportionally very considerably smaller than in the *Dicynodon* pelvis figured by Lydekker, and looks much less downwards than in that specimen. From the point where the ischium meets the ilium the posterior border curves downwards and then backwards, ending abruptly at the ischial tuberosity. From the tuberosity the lower border curves gently round to meet the pubis. The lower part of the ischium is flat except in being slightly concave in the neighbourhood of the obturator foramen. Round the posterior border of the acetabulum the ischium forms a prominent ridge, but the ridge formed by the ischium is not continuous with that formed by the pubis, a gap occurring at the ischio-pubic suture. From the acetabular border a prominent thickening or ridge runs backwards to the upper end of the ischial tuberosity.

There is no evidence of any marsupial bones, and from the condition of the skeleton this may almost be taken as conclusive proof that such bones did not exist in *Udenodon*. There is evidence, however, in favour of there having been a cartilaginous epipubis.

In *Udenodon baini* the ilium is very similar to that in *U. gracilis*, but the ischium is proportionally considerably larger though its general characters are very similar. The obturator foramen (*f.ob.*) is oval with the long axis directed antero-posteriorly and situated close under the border of the acetabulum. The long axis of the foramen measures about half the diameter of the neck of the ilium.

Femur.

In *Udenodon gracilis* the right femur has its posterior side well-displayed, and as its upper half has been broken loose its anterior side can also be examined with the exception of the head.

In its general proportions the femur (Plate XVII. fig. 5, *fm.*) agrees with that of the Monotremes, though in its characters it differs somewhat. It is much flattened throughout its whole length, and considerably broadened out both at its upper and lower ends. From the head to the greater trochanter the measurement is nearly three times as great as that across the middle of the shaft. From a little below the middle of the bone, the outer border forms an almost straight line to the top of the great trochanter. The inner border curves very markedly inwards to the head, and the curve is interrupted by the presence of the small trochanter, which forms a small but very distinct inwardly directed ridge. On the anterior surface of the bone so far as displayed is a small vertical groove a

little to the outside of the middle line; while to the inside of the great trochanter is a distinct but shallow concavity. On the posterior side of the bone there is a fairly deep concavity below the head and on the inner side of the small trochanter. On the outer edge of the posterior side there runs down, from a little below the great trochanter to beyond the middle of the shaft, a small sharp backwardly directed ridge. In the middle of the shaft a section is almost oval, showing a small but distinct medullary cavity. The lower end of the femur resembles very considerably the lower part of the bone in *Echidna* or *Ornithorhynchus*. The condyles are small and rather widely apart, and, as in the Monotremes, the whole lower end of the femur is much flatter than in the Eutherians. From the neighbourhood of the inner condyle an oblique ridge runs upwards and outwards towards the outer side of the middle of the shaft, apparently corresponding to the oblique ridge on the back of the lower end of the femur of *Echidna*.

In the skeleton of *Udenodon baini* (spec. 4) both femora are shown but in rather bad preservation, having been much crushed. The chief differences in this species are in the bone being proportionally stronger, in the greater development of the great trochanter, and in the small trochanter being less marked.

Tibia and Fibula.

In the skeleton of *Udenodon gracilis* (Pl. XVI.) both tibiæ and fibulæ are shown, but those of the left leg are not well displayed, and those of the right only show the posterior surface and have been slightly injured in clearing off the matrix.

The tibia (*tb.* Plate XVII. fig. 5) is considerably shorter than the femur, and resembles closely the tibia in *Echidna*. It is a moderately straight bone with a large flat head, a shaft tapering down to between the middle and lower thirds, and a distal end moderately dilated and with an oblique articular surface. It has a distinct though small medullary cavity.

The fibula (*fb.*) is a longer though more slender bone. As in Monotremes and most Marsupials the head is large, giving an articulation to the femur and having a portion passing up beyond the head of the tibia to give attachment to some of the leg-muscles. On passing downwards the fibula is directed slightly upwards, and it then curves inwards so as to form a wide interosseous space. At its lower end the bone is dilated considerably, and its articular surface is directed slightly inwards.

In *Udenodon baini* the tibia, like the femur, is proportionally a much stronger bone than in *U. gracilis*, and it is also proportionally shorter. The head is very large, and from it there runs down the front of the bone a very prominent crest. The fibula, as if to compensate for the greater strength of the tibia, is proportionally more slender than in the small species. It gives an articulation to the femur, but the head is much smaller and is scarcely extended beyond the level of the head of the tibia. It is

more curved than in *U. gracilis*, and there is thus formed a larger interosseous space.

There does not seem to have been an ossified patella in *Udenodon*.

Tarsus.

The tarsus of the right side (Pl. XVI.) has its under surface well shown, and though a dorsal view would have been more satisfactory, a good idea is obtained of the structure of the joint even though a little doubt may remain on one or two points. The tarsus of the left side is so twisted that it is difficult to be sure of some of the elements.

Articulating with the tibia and fibula respectively (Pl. XVII. fig. 5) are two large elements—manifestly the tibiale (*tl.*) and the fibulare (*fl.*), with a small bone lying between, doubtless the intermedium (*i.*). The distal row of the tarsus is formed by five tarsalia; while in the centre, between the distal row and the tibiale and fibulare, is a centrale (*c.*), small as displayed on the under surface, but probably of much larger size on the upper.

The tibiale, or astragalus, as displayed, is a fair-sized somewhat pentagonal bone with the upper and outer angle sharp and produced. By its proximal and probably its inner face it articulates with the tibia. On its outer face the little intermedium comes between it and the fibulare, but it is probable that an articulation between the two large elements takes place above and distally to the intermedium. On the distal border of the tibiale lies the small centrale. It is probable that the tibiale does not articulate with any other element. As the tarsus is displayed in the specimen, there appears to be no element between the 1st tarsale and the tibiale, and one might infer that the tarsale had articulated with the tibiale, and that these elements are slightly displaced; but it seems much more probable that what appears to be a very small centrale is merely a projection, showing on the under side, from a moderately large centrale which fits in between the 1st tarsale and the tibiale, as does the navicular in mammals.

The intermedium (*i.*) is a very small element, at least so far as displayed, fitting in between the tibiale and the fibulare, and articulating with these two elements and with the fibula. It is possible that the element may not be a true intermedium, but a small sesamoid bone; its being deeply implanted, however, between the other tarsal elements, and its occupying the exact position where an intermedium would be looked for, leads me to believe that I have rightly interpreted it as that.

The fibulare is a large, elongated, four-sided element, nearly as large as all the other tarsal elements together. Its proximal side, by which it articulates with the fibula, is the shortest of the four. The inner side, which is half as long again as the proximal, articulates with the intermedium, the tibiale, and the centrale. The distal end of the element, which is a little shorter than the inner side, but much broader than the proximal end, articulates with the fourth and fifth tarsalia and with the fifth metatarsal.

The centrale, as seen in the specimen, would appear to be a small element fitted in between the tibiale, the fibulare, and the third tarsale, but it seems probable that the dorsal view of the tarsus would show it to be a much larger element. This is rendered highly probable by the fact that there appears to be an unoccupied gap between the first tarsale and the tibiale. This must either have been occupied by the centrale or the 1st tarsale must have articulated with the tibiale, and in the specimen has been displaced. The positions occupied by the other tarsal elements lead me to favour the former alternative.

The 1st tarsale (*ts.* 1, Plate XVII. fig. 5) is a large element much resembling a metatarsal in shape. Its proximal end is expanded, and, assuming that it is in an undisturbed position in the specimen, the outer side of this end articulates with the 2nd tarsale. The proximal end must either articulate with the tibiale direct, or a portion of the centrale was interposed.

The 2nd tarsale is a very small element, articulating laterally with the 1st and 3rd tarsalia, and most probably with the centrale proximally. It gives support to the 2nd digit.

The 3rd tarsale is about twice as large as the 2nd. It articulates with the 2nd and 4th tarsalia and with the centrale, and gives support to the 3rd toe.

The 4th and 5th tarsalia (*ts.* 4, 5) are so closely united that there is some doubt as to whether the element present may not be entirely the 4th tarsale. The element is a somewhat oval-shaped bone with the distal side slightly concave. It fits in between the fibulare and the 3rd tarsale, and possibly articulates with the centrale. It gives support to the 3rd, 4th, and 5th metatarsals. Near its outer end there is an indication of a transverse suture, which seems to point to there being a small 5th tarsale closely united to, if not anchylosed with, the 4th. In dealing, however, with so small a structure, where the bones so closely resemble the matrix in colour that it is difficult at times to decide what is bone and what matrix, one cannot place much reliance on an indication so minute.

The hallux has a short quadrangular metatarsal (*mt.* 1) and a phalanx (*ph.*) almost exactly similar in shape and size, and a short ungual phalanx less than twice the length of the 1st phalanx.

The 2nd, 3rd, 4th, and 5th toes are so similar in all respects that a description of any one would suit, with very slight modifications, any of the others. In all four the metatarsals are elongated bones with rounded proximal ends, flattened distal ends, and with their shafts constricted in the middle. The first phalanx in all four toes is a quadrangular bone slightly longer than broad. In the fourth toe the phalanx is somewhat stouter than in the others. The second phalanx is a little shorter than the first, and very similar in all four toes. The ungual or terminal phalanx has in all five toes been provided with a short claw, only slightly curved.

Though the fore and hind limbs are fairly equal in length, the pes is very much smaller than the manus. All the digits are much

more feeble, and the claws have been only about one-third the size of those in the manus.

"PLATYPODOSAURUS ROBUSTUS, Owen."

In 1880 and 1881 Owen (8, 9) described in two papers parts of the skeleton of a large Anomodont reptile to which he gave the name of *Platypodosaurus robustus*. The remains comprised a number of vertebræ, a scapula, a humerus, the sternum, the greater part of the pelvis with the sacrum, a portion of one femur, and some phalanges. Unfortunately the head was missing. Owen recognized a number of affinities between the bones and those of *Dicynodon*, but was chiefly impressed by the many Mammal-like characters displayed, and particularly by the striking resemblances many of the bones showed to those corresponding in the Monotremes; and he suggests that the Monotremes may be the descendants of reptiles closely resembling *Platypodosaurus*.

Lydekker (7), in the 'British Museum Catalogue of Fossil Reptiles,' places *Platypodosaurus* among the Dicynodontia as a doubtful species, and expresses his opinion that from the general Dicynodont character of the specimens, the remains "are referable either to *Udenodon* or *Eudothiodon*."

As nothing has hitherto been known for certain of any of the bones of either *Udenodon* or *Eudothiodon* except the skull, no advance beyond Lydekker's position has been possible. Now, however, that the limb-bones of at least two species of *Udenodon* are known, it is possible to come nearer a solution of the *Platypodosaurus*-problem.

The chief distinctive features of the *Platypodosaurus* specimens are the great development in the humerus of the delto-pectoral crest which forms a downward projection, and the presence of a marked tricipital prominence. In *Udenodon gracilis* both of these characters are found, and the general proportions of the humerus are strikingly similar to those in *Platypodosaurus*. The sternum of *Platypodosaurus* does not differ greatly from that of *Udenodon baini*. The scapula agrees so closely with that of *U. baini* that had that of the latter been found alone it would almost certainly have been referred to a young specimen of *Platypodosaurus*. The femur of *Platypodosaurus*, so far as is known, differs somewhat from that of *U. gracilis*, especially in the greater development of the great trochanter, and in the less development of the small trochanter; but it agrees closely with the femur of *U. baini*. The pelvis of the larger anomodont, so far as it is preserved, agrees very closely with that of *U. gracilis* in its general proportions, and, if allowance be made for imperfections, probably also in its contours. The vertebræ differ very considerably from those of *U. baini* which I have figured. This is probably due to their belonging to different regions of the column in the two species.

From the close agreement between the bones of *Platypodosaurus* and those of *Udenodon gracilis* and *U. baini*, there seems to be

very little doubt that the *Platypodosaurus robustus* remains are the bones of a large species of *Udenodon*. The large skull figured by Owen (2) as *Udenodon magnus* bears almost the same proportion to the limb-bones of "*Platypodosaurus robustus*" that the skull of *Udenodon gracilis* does to its limb-bones. It seems, therefore, very probable that the bones described as *Platypodosaurus robustus* are parts of the post-cranial skeleton of *Udenodon magnus*, Owen. Lydekker (7), in his British Museum Catalogue, holds that *Udenodon magnus* is a synonym of *Udenodon prognathus* Owen. It is impossible for one away from the original specimens to offer an opinion on the subject, and though the figures seem to show a number of distinctive characters, Lydekker's work among the Anomodonts has been so carefully and conscientiously done, that any opinion expressed by him must always carry very great weight.

Affinities of Udenodon.

The genus most nearly allied to *Udenodon* is *Dicynodon*; in fact so great is the resemblance between the two genera that it has been suggested that *Udenodon* was the female of *Dicynodon*. The discovery of the limb-bones shows that the two genera are distinct though very closely related; and there seems to be very little doubt that *Udenodon* is merely a slightly modified *Dicynodon* in which the tusks have ceased to develop.

When the bones of *Udenodon* or *Dicynodon* are compared with those of other Vertebrates, we find that the group has many marked affinities with the Theriodonts and the Mammals; some affinities, but less marked, with the primitive reptilian types such as *Pariasaurus*, and even with the Rhynchocephalians, Plesiosaurs, and Chelonians; but that the relationships with the more highly specialized reptiles, such as the Crocodiles, Dinosaurs, and Pterodactyles, are rather remote.

In *Udenodon* the anterior half of the skull is so greatly modified in connection with the toothless beak that the affinities are masked. There is little doubt, however, that the beak is derived from that of a Theriodont type, intermediate stages being found in *Cryptocynodon* and *Dicynodon*.

In the structure of the posterior part of the skull *Udenodon* agrees closely with the Theriodonts and Mammals; and differs markedly from all the regular Reptilian types.

In the majority of typical reptiles the temporal region of the skull is protected by two bony arches—a supra-lateral arch formed by the postfrontal or postorbital and the squamosal or supratemporal, and an infra-lateral formed by the jugal and quadratojugal. This arrangement, or a modification of it, occurs in the Rhynchocephalians, Pelycosaurians, Crocodilians, Dinosaurs, and other groups. The more primitive lizards differ in having lost the lower arch. In the Dicynodonts, as in the Theriodonts and Mammals, there is but a single arch formed by the jugal and squamosal; and some difference of opinion has been held as to

whether this single arch is the homologue of the upper or of the lower arch in the typical reptiles. As, however, the single arch in the Dicynodonts differs in structure from either of the normal reptilian arches, and as it is moderately certain that the reptiles with the two arches have been derived from the ancestral forms which had the temporal region completely roofed, by quite a different line from that by which the Dicynodonts have arisen, the single arch in the latter cannot be regarded as homologous with either of the arches in the more typical reptile. In the branch which gave rise to the majority of Reptilian orders the temporal roof became transformed on either side into a couple of arches by an upper fenestra formed between the parietal, squamosal, postorbital, and postfrontal, and a lower fenestra between the jugal, quadrato-jugal, supratemporal[1], and postorbital. In the other great Reptilian branch which gave rise to the Anomodonts, Theriodonts, and Mammals, a single fenestra only has been formed in the temporal roof, corresponding to the upper fenestra of the branch from which the Rhynchocephalians and allied forms have sprung. After the formation of the fenestra, or possibly before, the skull in the anomodont line became much simplified by the reduction and loss of a number of elements and the corresponding increase in size of others. The squamosal increased apparently early in relative size, and with its increase the supratemporal and the quadrato-jugal became first reduced and then lost. In a number of different lines of descent we find a similar process has gone on. Thus, in *Sphenodon* the squamosal by its increase has led to the complete loss of the supratemporal and the great reduction of the quadrato-jugal; in *Aëtosaurus* the increased development of the squamosal has led to the loss of both the supratemporal and the quadrato-jugal; and in the Plesiosauria, which are possibly an offshoot from the Anomodont stem, we find a very large squamosal with complete loss of the supratemporal and quadrato-jugal. The temporal region of *Udenodon* only differs from that in the Plesiosaur in that, whereas the latter has both a postfrontal and a postorbital, one of those elements is lost in the former; in my opinion it is the postorbital which is lost in the Anomodont.

The only essential difference between the structure of the postero-lateral region of the skull in the Mammals and that in the Anomodonts and Theriodonts is that the mammalian skull has become further simplified by the loss of the postfrontal and the almost complete loss of the quadrate. A number of years ago I advanced (10) the view that the reptilian quadrate had its

[1] Concerning the two bones found in the upper and posterior temporal region, opinions have differed as to which is to be regarded as the squamosal and which supratemporal. The opinion to which I have been led is that it is invariably the upper and inner which is the squamosal—an opinion which agrees with that of Baur, but differs from that of most British authorities, including Parker. When only the one element is found it appears to be always the squamosal.

homologue in the mammal in the interarticular cartilage of the lower jaw. If recent advances in palæontology have not fully confirmed this view, they have at least shown that practically all the alternative theories are untenable.

In the higher Theriodonts, e. g. *Cynognathus*, the zygomatic arch, though composed of the same elements as in *Udenodon*, differs very greatly in the relative proportions of the parts; but in the lower Theriodonts, i. e. *Ictidosuchus* (11), the zygomatic arch bears much resemblance to that in the Anomodonts.

The palate in *Dicynodon* and *Udenodon* differs considerably from the normal reptilian type, and agrees essentially with that in the Theriodonts and Mammals.

All known Reptiles have palates more or less modified from a primitive type such as is found in *Pariotichus* or *Procolophon*, and which consists of the following elements:—an anterior pair of bones which meet in the middle line, and which are usually regarded as "vomers"; a pair of large pterygoids, which have each a posterior and outer branch to the quadrate, an outer and anterior branch joining the transpalatine, and an anterior and inner branch which usually meets the so-called "vomer"; a pair of palatines lying on the outer side of the anterior and inner branches of the pterygoids; a pair of transpalatines; and a median element passing forwards from the basisphenoid between the two pterygoids, and usually referred to as the "parasphenoid." This arrangement we find with only slight modifications in all the early groups, including types so dissimilar as *Pareiasaurus*, *Procolophon*, *Ichthyosaurus*, *Plesiosaurus*, *Dimetrodon*, and *Sphenodon*.

The palates of the Theriodonts and Anomodonts are very considerably modified derivatives of the same type. Unfortunately in none of the primitive Theriodonts is the palate at all well known. We know, however, that a secondary palate was not formed in either *Gorgonops* or *Ictidosuchus*, nor apparently in *Ælurosaurus*. In *Udenodon* we have an imperfect secondary palate, and in the higher Theriodonts a secondary palate as well-developed as that in mammals, and essentially similar to that in mammals. As the general structure of the skeleton of *Udenodon* is essentially Theriodont, and as the palate only differs from that of the typical Theriodont in the specialization of the beak and in the secondary palate being imperfect, one is justified in concluding that the Anomodonts are a specialized offshoot from the earlier Theriodonts. In the evolution of the Theriodont palate from the primitive Reptilian type, the changes which have taken place appear to have been the following:—The anterior and internal branch of the pterygoid has become greatly reduced and finally lost, and its place and function to a large extent has been taken up by a great increase in the so-called "parasphenoid"; while the anterior and outer branch has become more developed, and with its increase the palatine has come to lie rather internal than external to the pterygoid. With the development of a secondary

palate the anterior paired element—the so-called "vomer"—being no longer required as a bony floor for the nasal cartilages, has become reduced, and is only retained to give support to the cartilages of Jacobson's organ. This is the condition we find in *Gomphognathus* (12). The "parasphenoid," having now a new function—that of forming a support for the secondary palate—becomes greatly developed as a median plate, which is unquestionably the homologue of the mammalian vomer. From this it follows that the element called *Parasphenoid* in the Reptiles generally ought to be called the *Vomer*; while the anterior paired element, usually regarded as the "vomer," but which is the homologue of the dumbbell-shaped bone in *Ornithorhynchus*, may be called the "anterior vomer," or by the name I have elsewhere (13) proposed for convenience, the *Prevomer*.

In *Udenodon* the true vomer is greatly developed, but the anterior vomer or prevomer is lost—no doubt owing to the great palatal development of the premaxillary. The vomer in the Anomodonts agrees with the mammalian vomer even more closely than does the vomer in the higher Theriodonts.

In the Chelonians, probably as the result of a parallel development, the palate bears considerable resemblance to that in the Anomodonts, and it even appears that the median vomer is a true vomer, as in *Dicynodon* and its allies.

The lower jaw of *Udenodon* differs greatly in appearance from that in the Theriodonts, owing to its being toothless and to the absence of a well-developed coronoid process. As the elements are apparently the same, the difference is probably due largely to a degeneration in the Anomodont jaw, similar to that which has taken place in the toothless mandibles of such mammals as Echidna or the Whales.

The vertebræ appear to be essentially similar in structure in the Anomodont and in the Theriodont; but in the Anomodont the type is somewhat more primitive, in that the ribs of the lower trunk vertebræ are not specialized as they are in the higher Theriodont at least.

The shoulder-girdle in *Udenodon* belongs to the type which is found to persist with little variation from the lower forms such as *Pareiasaurus* up to the Monotremes. The cartilaginous elements consist of a scapula, a coracoid, and a distinct precoracoid, while the membrane-bone elements are a clavicle, a supra-clavicle or cleithrum, and a median interclavicle. In the Anomodonts the coracoid and the precoracoid are extremely like those in the Theriodonts, both the higher and the lower; but, curiously enough, the scapula agrees with that in the higher Theriodonts such as *Cynognathus*, and differs from that in the lower Theriodonts, e. g. *Ictidosuchus*, in having a moderately well-developed acromion.

The humerus closely resembles that in the Theriodonts, but whereas in the latter, as in the typical terrestrial mammals, the humerus is elongated, in the Anomodonts, as in the Monotremes,